
SIMULATED DRY MATTER YIELDS FOR ASPEN AND SPRUCE STANDS IN THE NORTH AMERICAN BOREAL FOREST

by
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RÉSUMÉ

La production primaire nette (PPN exprimée par $\text{g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$) peut être calculée à partir du total annuel de rayonnement solaire quotidien utilisé pour la photosynthèse active (RSQPA exprimé par $\text{MJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) multiplié par le rendement en matière sèche par unité de radiation de photosynthèse [ϵ exprimé par $\text{g} \cdot \text{MJ}^{-1}$ (souvent appelé efficacité de radiation)]. Le RSQPA peut être mesuré par télédétection en utilisant l'indice de végétation par différence normalisée (NDVI). Nous avons utilisé un modèle de simulation d'écosystème, BIOME-BGC, que nous avons adapté pour des peuplements d'espèces du genre **Picea** (épinette) et du genre **Populus** (tremble) en vue de déterminer les variables importantes influant sur la valeur de ϵ en climat boréal. La photosynthèse annuelle et l'intensité respiratoire totale étaient plus élevées dans le cas du tremble, tandis que la PPN était supérieure dans le cas de l'épinette, aux deux sites. Les variables de peuplement, comme la biomasse des tiges et l'indice de surface foliaire, ont eu des effets importants sur la valeur simulée de ϵ pour les deux genres, effets qui se sont traduits par une augmentation de l'intensité respiratoire et de la photosynthèse respectivement. Au contraire, les variables de forme de relief, comme la pente et l'orientation, ont eu peu d'effet sur la valeur simulée de ϵ . La variation annuelle de la valeur simulée de ϵ a été corrélée avec la quantité de précipitation annuelle pour les deux genres à la lisière sud de la forêt boréale (Prince-Albert, Saskatchewan) ainsi qu'à la lisière nord (Thompson, Manitoba). Pour une quantité donnée de précipitation, la valeur de ϵ pour l'épinette et le tremble était supérieure à Prince-Albert en raison d'une période de croissance plus longue (augmentation de la PPN). Ces simulations laissent croire qu'une valeur constante de ϵ ne peut pas être utilisée pour déterminer la PPN de forêts boréales à partir du RSQPA mesuré par télédétection.

SUMMARY

Net primary production (NPP, $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) may be calculated from the annual sum of daily absorbed photosynthetically active radiation (APAR, $\text{MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) multiplied by the dry matter yield of photosynthetically active radiation [ϵ , $\text{g} \cdot \text{MJ}^{-1}$ (often called radiation use efficiency)]. APAR may be remotely sensed using the Normalized Difference Vegetation Index (NDVI). We used an ecosystem process simulation model, BIOME-BGC, parameterized for stands of **Picea** species (spruce) and **Populus** species (aspen), to determine the important variables affecting ϵ in boreal climates. Annual photosynthesis and total maintenance respiration were individually greater for aspen, whereas NPP was greater for spruce at both sites. Stand variables such as stem biomass and leaf area index had large effects on the simulated value of ϵ for both genera by increasing the amount of maintenance respiration and photosynthesis, respectively. In contrast, landscape variables such as slope and aspect had little effect on simulated ϵ . Year-to-year variation in simulated ϵ was correlated with annual precipitation for both genera at the southern edge of the boreal forest (Prince Albert, Saskatchewan) and at the northern edge (Thompson, Manitoba). For a given amount of precipitation, spruce and aspen had higher ϵ at Prince Albert due to a longer growing season (increasing NPP). These simulations suggest that a constant ϵ may not be used to determine NPP for the boreal forest from remotely sensed APAR.

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INTRODUCTION

Annual net primary production (NPP, g m⁻² year⁻¹) may be determined over large regions with satellite sensors such as the Advanced Very High Resolution Radiometer using the Normalized Difference Vegetation Index [NDVI, (near-infrared band — red band)/(near-infrared band + red band)] to calculate the fraction of incident photosynthetically active radiation (PAR) absorbed by the foliage (Asrar *et al.*, 1984; Goward and Huemmrich, 1992). NPP is related to the annual sum of absorbed photosynthetically active radiation (APAR, MJ m⁻² day⁻¹) by:

$$\text{NPP} = \epsilon \Sigma (\text{APAR}) = \epsilon \Sigma (\text{NDVI} \cdot \text{PAR}) \quad (1)$$

where: ϵ (g/MJ) is the dry matter yield of photosynthetically active radiation (Monteith, 1977; Russell *et al.*, 1989; Prince, 1991). Dry matter yield is often termed radiation use efficiency, although Russell *et al.* (1989) and Prince (1991) suggest this term is inappropriate as true thermodynamic efficiencies are dimensionless. Running and Hunt (in press) found that measured values of ϵ for woody vegetation are significantly lower than those for herbaceous vegetation (Prince, 1991), and they speculated that the cause of lower ϵ may be the maintenance respiration by woody biomass.

Both Prince (1991) and Running and Hunt (in press) report considerable scatter in the measured values of ϵ ; much of this scatter may be related to climate (Hunt and Running, 1992). To determine how ecosystem type may affect ϵ , we generalized the logic from the coniferous forest simulation model, FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991), to develop a new model, BIOME-BGC (Running and Hunt, in press). FOREST-BGC is well validated with a variety of experimental data (McLeod and Running, 1988; Nemani and Running, 1989; Hunt *et al.*, 1991; Korol *et al.*, 1991), and hence a good platform for further model development. One of the major differences between FOREST-BGC and BIOME-BGC is the physiological treatment of photosynthesis based on the model of Farquhar *et al.* (1980) and von Caemmerer and Farquhar (1981). This change allows both parameterization from readily available leaf gas-exchange data and provides more confidence in predicting ecosystem response to climatic change and increased atmospheric CO₂.

One of the ecosystems that may be greatly affected by climatic change is the boreal forest (Harrington, 1987). Furthermore, Tans *et al.* (1990) suggest that northern forests may be a large sink for increased atmospheric CO₂. A major experiment being planned by Canada and the United States is the Boreal Ecosystem Atmosphere Study, BOREAS (BOREAS Science Steering Committee, 1990) with a goal of developing algorithms for remotely sensing NPP. We simulated ϵ for two genera, spruce (*Picea* species) and aspen (*Populus* species) for a typical southern boreal forest climate (Prince Albert, Saskatchewan) and a typical northern boreal forest climate (Thompson, Manitoba). Our objective was to determine the ecosystem variables that may have the largest effects on ϵ and, hence, estimated NPP by remotely sensed APAR.

MODEL DESCRIPTION

The major difference between BIOME-BGC (Running and Hunt, in press) and FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991) is the treatment of canopy photosynthesis. The current model uses the equations from Farquhar *et*

al. (1980) and Leuning (1990). First the CO₂ compensation point in the absence of dark respiration (Γ^* , Pa) is calculated:

$$\Gamma^* = 0.5 \text{ O} / \tau \quad (2)$$

where: O is the atmospheric O₂ concentration (Pa) and τ is the ribulose biphosphate carboxylase-oxygenase (Rubisco) specificity factor (Pa/Pa). The rate of CO₂ fixation by Rubisco (V , $\mu\text{mol m}^{-2} \text{ s}^{-1}$) is calculated from two equations:

$$V = (1 - \Gamma^* / C) V_{\text{max}} C / [C + K_c(1 + \text{O} / K_o)] \quad (3a)$$

$$V = g_c(\text{Ca} - C) / P \quad (3b)$$

where: C is the intercellular CO₂ concentration (Pa); V_{max} is the maximum rate of Rubisco; K_c and K_o are the Michaelis-Menton coefficients (Pa) of Rubisco for CO₂ and O₂, respectively; P is the atmospheric pressure (Pa); and g_c is the leaf conductance to CO₂ ($\text{mol m}^{-2} \text{ s}^{-1}$). Kinetic parameters for Rubisco were obtained from Woodrow and Berry (1988). Equations 3a and 3b are combined with the elimination of C and solved for V by the quadratic equation (Leuning, 1990).

The rate of CO₂ fixation limited by the regeneration of ribulose biphosphate (J , $\mu\text{mol m}^{-2} \text{ s}^{-1}$) is calculated from two equations:

$$J = (1 - \Gamma^* / C) J_{\text{max}} (C - \Gamma^*) / (C + 2\Gamma^*) \quad (4a)$$

$$J = g_c(\text{Ca} - C) / P \quad (4b)$$

where: J_{max} is the maximum rate of ribulose biphosphate regeneration in terms of CO₂ uptake. Equations 4a and 4b are combined and solved for J by the quadratic equation (Leuning, 1990). J_{max} and V_{max} are calculated from leaf nitrogen concentration (Evans, 1989; Friend, 1991). Biochemical parameters other than J_{max} and V_{max} may be more or less constant for C₃ plants, especially over large areas for which this model is applicable, so we have reduced the biochemical complexity of photosynthesis to a series of constant parameters and one major variable, leaf nitrogen concentration.

The maximum rate of photosynthetic CO₂ uptake (A_{max} , $\mu\text{mol m}^{-2} \text{ s}^{-1}$) at the optimum temperature is calculated from the minimum of either J or V :

$$A_{\text{max}} = \min\{J, V\} \quad (5)$$

A_{max} is adjusted for daytime-average air temperature to obtain A' using an equation in Lassiter (1975), and the instantaneous rate of leaf maintenance respiration (which also depends on daytime-average air temperature with a Q_{10} of 2.0) is subtracted from A' .

The quantum efficiency of photosynthesis (α , mol CO₂/mol photon) to PAR is calculated by:

$$\alpha = \phi (C - \Gamma^*) / (C + 2\Gamma^*) \quad (6)$$

where: ϕ is the maximum quantum efficiency. Maximum instantaneous PAR was calculated from atmospheric transmissivity, estimated by the model MT-CLIM (Running *et al.*, 1987), and equations from Gates (1980). Next, the average canopy photosynthetic rate (A , $\mu\text{mol m}^{-2} \text{ s}^{-1}$) is calculated as in Rastetter *et al.* (1992):

$$A = (A' / \kappa L^*) \ln\{[A' + \alpha \text{ PAR}] / [A' + \alpha \text{ PAR} \exp(\kappa L^*)]\} \quad (7)$$

where: L^* is the one-sided leaf area index and κ is the extinction coefficient. BIOME-BGC uses all-sided leaf area index (LAI, from its conifer heritage) so one-sided L^* is determined from all-sided LAI. Finally, total daily canopy net photosynthesis (PSN, $\text{kg C ha}^{-1} \text{ day}^{-1}$) is calculated from:

$$\text{PSN} = A \text{ LAI } (0.85 \text{ daylength}) (12 \times 10^{-5}) \quad (8)$$

where: 0.85 is a constant determined from the integration of A (from Equation 7) over a day and (12×10^{-5}) converts units.

Canopy APAR was calculated from one-sided L^* :

$$\text{APAR} = \text{PAR} [(1-r - \exp(\kappa L^*))] \quad (9)$$

where: r is the fraction of incident PAR reflected from the canopy (Jarvis and Leverenz, 1984; Goward and Huemmrich, 1992). Incident PAR was assumed to be one-half of the incident daily shortwave radiation from the model, MT-CLIM (Running *et al.*, 1987). NPP was calculated as (PSN — total growth respiration — total maintenance respiration); ϵ was calculated as $\text{NPP}/\Sigma(\text{APAR})$. To convert ϵ from grams carbon to grams dry matter, we assumed the carbon content of dry matter was 45 per cent.

Another difference between BIOME-BGC and FOREST-BGC is that we defined a new state variable, fine root biomass (kg C/ha), which is "grown" on a given yearday and "shed" on a subsequent yearday. This was done so physiological measurements of root maintenance respiration could be used to parameterize BIOME-BGC. For multiple-year simulations, a carbon storage term was incorporated so growth for the current year would be affected by photosynthesis from the previous year (Hunt *et al.*, 1991). A fraction of the current year's net carbon gain (canopy net photosynthesis — total maintenance respiration) is subtracted and saved for the next year, and the previous year's carbon storage is then added to the current year's net carbon gain.

Table 1.
BIOME-BGC Physiological Parameters.

Name	Spruce	Aspen
Specific leaf area ($\text{m}^2/\text{kg C}$)	27 ^c	55 ^d
Canopy extinction of PAR (κ)	-0.5 ^e	-0.5 ^e
Canopy reflectance of PAR	0.025	0.05
Leaf nitrogen content (%)	0.9 ^{fg}	2.0 ^g
Optimum temperature ($^{\circ}\text{C}$)	20 ^h	25 ^{jk}
Stressed leaf water potential (MPa)	-1.7	-1.7
Max. stomatal conductance (mm/s)	1.5	5.0 ⁱ
Boundary layer conductance (m/s)	1.0	1.0
All-sided LAI/1-sided L^*	2.3 ^c	2.0
Leaf R_m^a ($\text{kg C kg}^{-1} \text{ C day}^{-1}$)	0.002 ^h	0.009 ^k
Stem R_m ($\text{kg C kg}^{-1} \text{ C day}^{-1}$)	0.00003 ^l	0.00004 ^m
Coarse root R_m ($\text{kg C kg}^{-1} \text{ C day}^{-1}$)	0.0003	0.0003
Fine root R_m ($\text{kg C kg}^{-1} \text{ C day}^{-1}$)	0.002 ⁿ	0.009 ^o
Q_{10} for R_m	2.0	2.0
Leaf R_g^b (kg C/kg C)	0.30	0.30
Stem R_g (kg C/kg C)	0.25 ^l	0.25
Root R_g (kg C/kg C)	0.30	0.30 ^o
PSN fraction to next year (%)	25 ^q	25 ^q
Leaf allocation (%)	15 ^{cr}	30 ^{cr}
Stem allocation (%)	35 ^{cr}	35 ^{cr}
Coarse root allocation (%)	25 ^s	17.5 ^s
Fine root allocation (%)	25 ^s	17.5 ^s

Notes: a. maintenance respiration; b. growth respiration; c. Cannell, 1982; d. Jurik, 1986a; e. Jarvis and Leverenz, 1984; f. Hom and Oechel, 1983; g. Flanagan and Van Cleve, 1983; h. Vowinkel *et al.*, 1975; i. Jurik, 1986b; j. Jurik *et al.*, 1988; k. Lawrence and Oechel, 1983b; l. Ryan, 1990; m. Foote and Schaedle, 1976; n. Johnson-Flanagan and Owens, 1986; o. Lawrence and Oechel, 1983a; p. Ledig *et al.*, 1976; q. Hunt *et al.*, 1991; r. Van Cleve *et al.*, 1983; s. Raich and Nadelhoffer, 1989.

METHODS

The simulations for Prince Albert, Saskatchewan and Thompson, Manitoba, started with a snowpack of 65 mm and a soil water content of 45 mm on yearday 1 (January 1), with a total available water content of 150 mm, typical of a well-drained site (Viereck *et al.*, 1986). For the carbon budget analyses of both genera, we used all-sided LAI's of 5.0 at Prince Albert and LAI's of 3.0 at Thompson. We used the following values: stem biomass of 20 Mg C/ha, coarse root biomass of 2 Mg C/ha, and fine root biomass of 1 Mg C/ha, which are within the range of values for the North American boreal forest (Cannell, 1982). However, to equalize the starting conditions for both sites in order to simulate the possible importance of stand, site, and climate variables, we set the LAI at 5.0 for subsequent model runs. For multiple-year simulations, the snowpack and soil water content on yearday 1 were carried over from the previous year, but LAI and biomass were kept the same so forest growth over time would not affect the value of ϵ (Hunt *et al.*, 1991).

We parameterized BIOME-BGC from the published data on aspen and spruce (Table 1). When the data were not available for these genera, we either used the parameter from the other genus or used data from related genera. One of the largest differences between aspen and spruce is the specific leaf area (Table 1), which is a sensitive parameter in BIOME-BGC. Rates of maintenance respiration of leaves and roots were higher for aspen; the photosynthetic capacity of aspen stems reduced the

carbon lost from respiration (Foote and Schaedle, 1976) so the daily rate is only slightly greater than spruce (Table 1). Above-ground allocation for both genera was from Cannell (1982) and Van Cleve *et al.* (1983); using the data in Raich and Nadelhoffer (1989) and Van Cleve *et al.* (1991, using the high values for annual production), we calculated about 50 per cent of the carbon will be allocated belowground for a spruce stand and 35 per cent of the carbon will be allocated belowground for an aspen stand. Because we used the same growth respiration for both fine and coarse roots, we arbitrarily divided the total equally between fine roots and coarse roots (Table 1).

We obtained climatic data of Prince Albert and Thompson from the Canadian Climate Centre (CCID, Downsview, Ontario). The yeardays for the start and end of the growing season were defined as when the expected minimum temperature was equal to 0°C (Figure 1). The expected minimum temperature was calculated using a second-order polynomial least-squares regression (Chatterjee and Price, 1977) of daily minimum air temperatures with yearday for the year 1988. The standard error of the y -estimate was 7.2°C for Prince Albert and 7.7°C for Thompson. The start and end of the growing season determine when the fine roots of both genera and the leaves of aspen are "grown" and "shed." At Prince Albert, the growing season began on yearday 107 (16 April) and ended on yearday 276 (2 October); whereas at Thompson, the start and end of the growing season were yeardays 133 (12 May) and 250 (7 September), respectively (Figure 1). The definition of growing season by polynomial regression is only one of several different methods that may be used.

Using the above yeardays for the growing season, we estimated the effect that year-to-year variations in climate would have on ϵ . We performed a least-squares regression of ϵ with annual precipitation. The effect of site on the regression for each genus was tested using a dummy variable set to 0 for Prince Albert and 1 for Thompson (Chatterjee and Price, 1977). For single-year simulations, we used climatic data for the year 1988, which had annual precipitations (36.6 and 37.5 cm for Prince Albert and Thompson, respectively) close to the long-term averages for both sites.

RESULTS AND DISCUSSION

Simulated Carbon Budgets

Simulations with 1988 climate data show spruce had a higher cumulative net carbon gain than aspen for both sites (Figure 2).

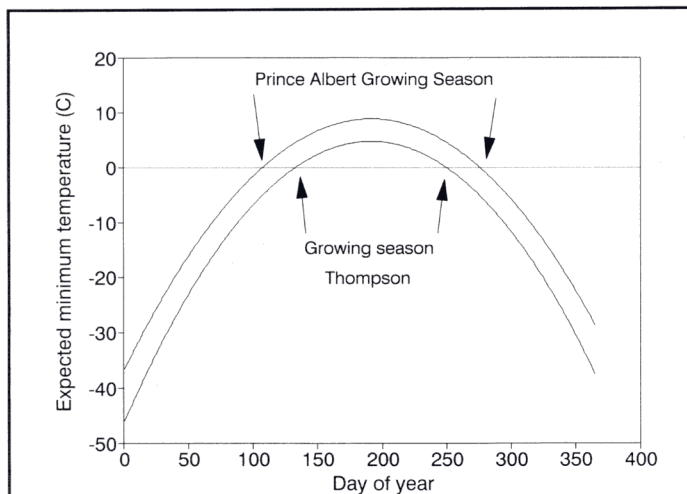


Figure 1. Determination of growing season at Prince Albert, Saskatchewan, and Thompson, Manitoba. Expected minimum air temperature was calculated using a second-order polynomial regression of minimum air temperature and yearday. The start and end of the growing season is defined as when the expected minimum temperature was equal to 0°C.

Table 2. Simulated Annual Carbon Budgets.				
	Prince Albert ^a		Thompson ^b	
	Spruce	Aspen	Spruce	Aspen
net photosynthesis ^c	12150	14926	5424	5887
maint. respiration ^c	1783	6684	1234	4007
growth respiration ^c	2929	2328	1184	531
net primary production ^c	7438	5914	3006	1349
APAR (MJ m ⁻² yr ⁻¹)	936	768	584	397
ϵ (g/MJ)	1.59	1.54	1.03	0.68

^a LAI = 5.0
^b LAI = 3.0
^c units are kg C ha⁻¹ year⁻¹

The maximum photosynthesis rates (A_{max} , Equation 5) were about $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ for spruce and $6 \mu\text{mol m}^{-2} \text{s}^{-1}$ for aspen on an all-sided leaf area basis. These values are comparable to those in the literature (Vowinckel *et al.*, 1975; Hom and Oechel, 1983; Lawrence and Oechel, 1983b; Jurik, 1986a; Jurik *et al.*, 1988). Furthermore, total season net photosynthesis for aspen was greater compared to spruce, but aspen had greater annual maintenance respiration (Table 2), so cumulative carbon gain and NPP for aspen were less than for spruce (Figure 2, Table 2). The differences in annual net photosynthesis (and, hence, growth respiration) for the same genus between the two sites were almost

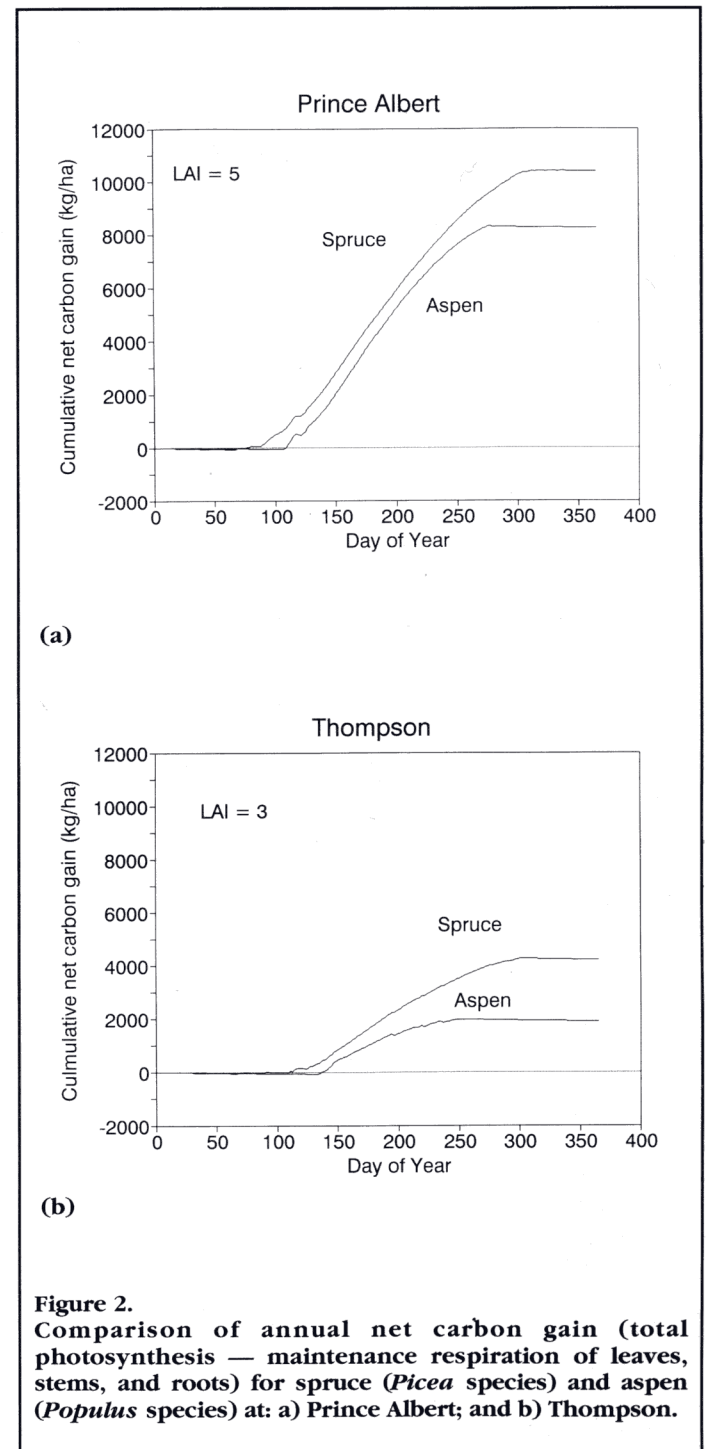
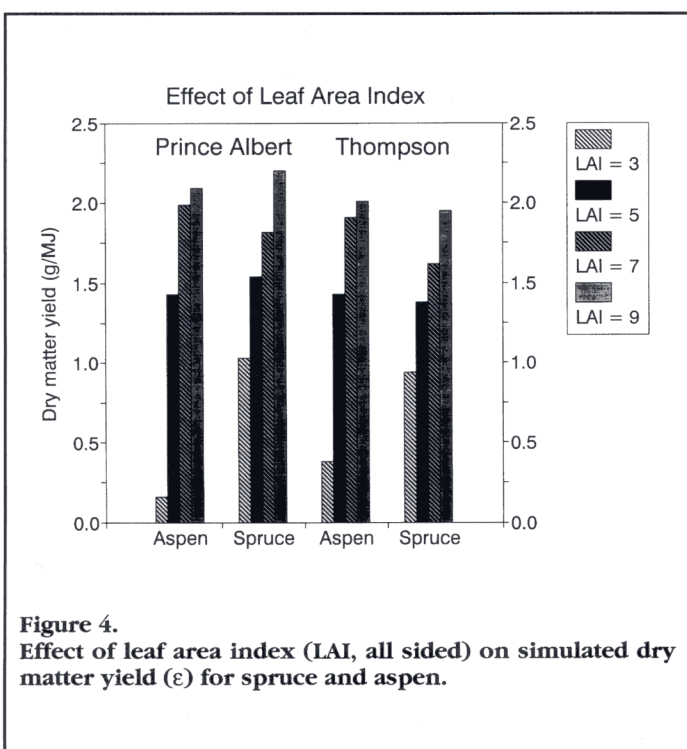
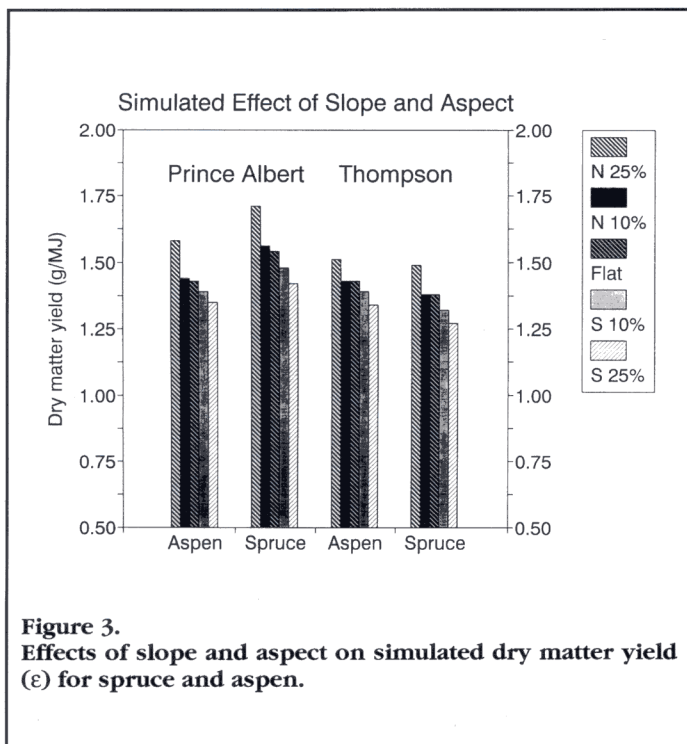


Figure 2. Comparison of annual net carbon gain (total photosynthesis — maintenance respiration of leaves, stems, and roots) for spruce (*Picea* species) and aspen (*Populus* species) at: a) Prince Albert; and b) Thompson.



little PAR is absorbed over the winter months due to low solar altitudes). As a result, greater NPP and APAR for spruce at Prince Albert caused simulated ϵ (1.59 g/MJ) to be about equal to ϵ for aspen (1.54 g/MJ). At Thompson, ϵ for spruce (1.03 g/MJ) was greater than ϵ for aspen (0.68 g/MJ) because simulated NPP was much greater for spruce.

Analysis of Dry Matter Yield (ϵ)

Slope and aspect had consistent but small effects on simulated ϵ for both genera at both sites with higher ϵ for north-facing slopes (Figure 3). However, NPP and APAR were lowest on north-facing slopes and highest on south-facing slopes. For example, at Prince Albert, simulated NPP on 25 per cent north-facing slopes were 7094 and 5816 kg C ha⁻¹ year⁻¹ for spruce and aspen, respectively, whereas for 25 per cent south-facing slopes, spruce had NPP of 7474 and aspen had NPP of 5936 kg C ha⁻¹ year⁻¹. With higher amounts of PAR, canopy net photosynthesis on south-facing slopes were nearly light saturated (Equation 7) so increased APAR would not increase photosynthesis. As the variation in slope across the landscape at Thompson and Prince Albert is mostly less than 10 per cent (from topographic maps of Nelson House, Manitoba, and Prince Albert National Park, Saskatchewan, respectively), so these simulations suggest topography may not be a significant variable affecting ϵ .

Changes in the all-sided LAI caused large changes on the simulated ϵ (Figure 4) for the given initial values of stem and root biomass. At low LAI, canopy net photosynthesis was light saturated, decreasing ϵ in a similar manner as did the effect of south-facing slopes. At high LAI, increased PAR penetrated through the canopy where the rate of leaf photosynthesis was not light saturated. Aspen approached a maximum ϵ at LAI of 7 and 9, at which point the increase in leaf maintenance respiration equalled the increase in canopy net photosynthesis (Figure 4). With lower rates of leaf maintenance respiration, a maximum LAI for spruce was not apparent (Figure 4).

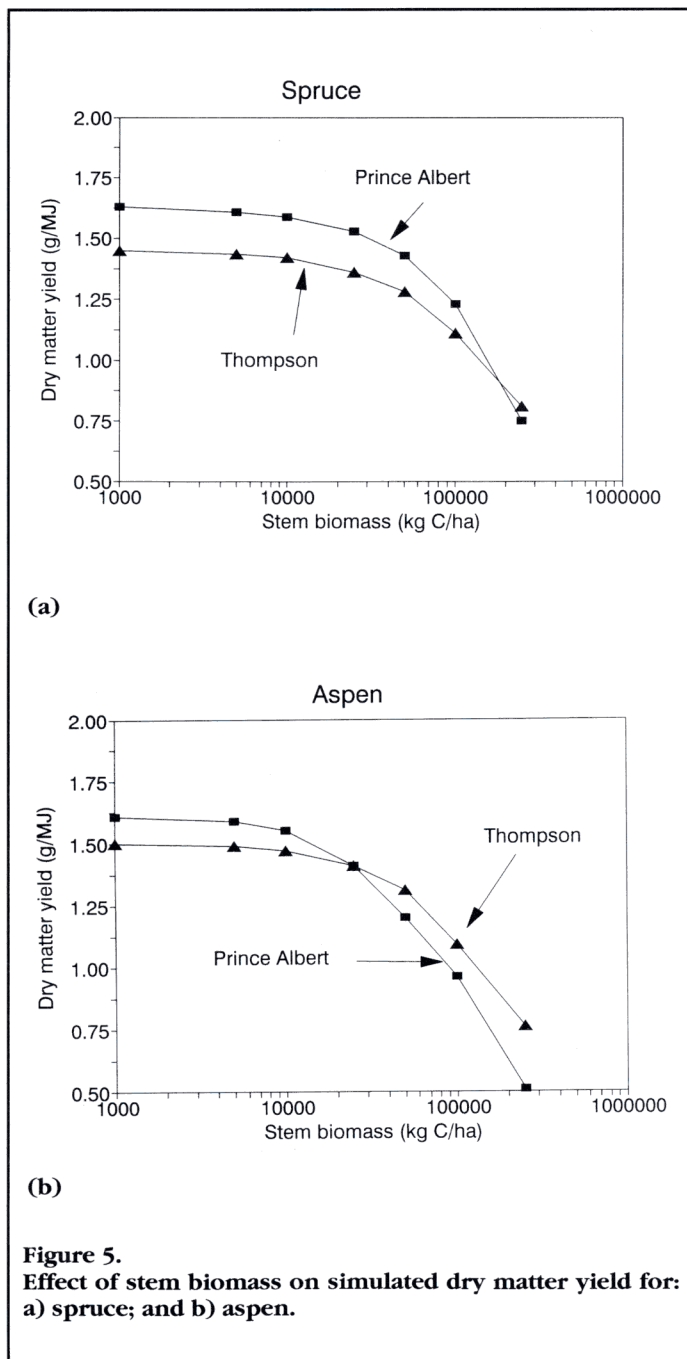
Another variable that varies across the landscape is the maximum available soil water content, which is determined by both soil texture and soil depth. Simulation with various maximum available soil water contents from 25 mm to 300 mm for both genera at both sites indicated that only at the lowest water content (25 mm) was ϵ reduced by more than 10 per cent (simulations not shown). This was due to the frequent rains during the summer (56 per cent of total precipitation in Prince Albert and 54 per cent at Thompson), which kept the soil sufficiently moist.

The total amount of maintenance respiration was greatly increased by increasing the mass of woody stems, reducing ϵ by more than 50 per cent (Figure 5). At low stem biomass, aspen stands had higher ϵ at Prince Albert. However, with increasing stem biomass of aspen, ϵ at Thompson was greater than ϵ at Prince Albert (Figure 5). This interaction between stem mass and climate also occurred in the spruce simulations, but the differences were not as dramatic (Figure 5). Hunt and Running (1992) suggested that this occurred because of a temperature effect on total maintenance respiration; colder temperatures at Thompson decreased simulated stem maintenance respiration compared to Prince Albert.

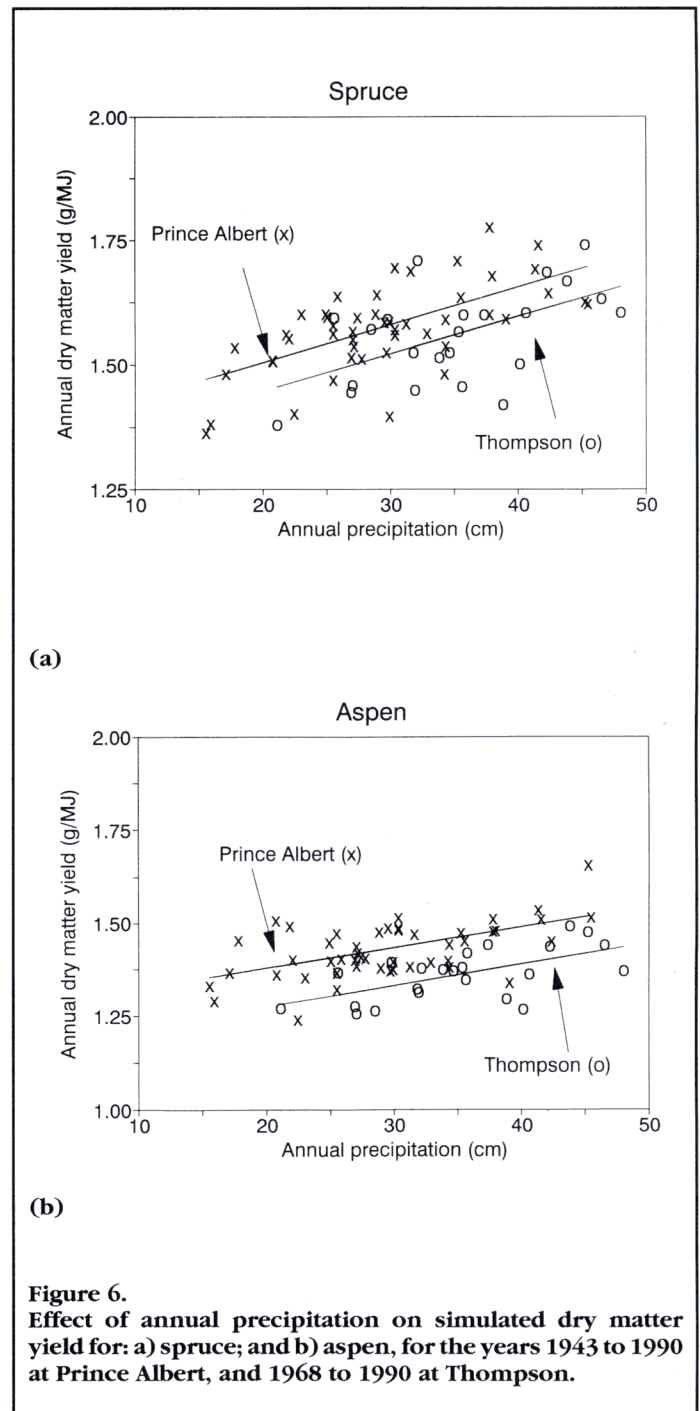
Multiple-year simulations were run over the period from 1943 to 1990 for Prince Albert and from 1968 to 1990 for Thompson to determine how ϵ for spruce and aspen stands may vary due to year-to-year differences in climate. NPP and ϵ were correlated with annual precipitation for both genera at both sites (Figure 6). The regression equations for the two sites have significantly different y -intercepts ($P > 0.95$), whereas the slopes are equal (Figure 6). For spruce, the coefficient of determination (R^2) is 0.41 for Prince Albert and 0.31 for Thompson, whereas for aspen, the R^2 is 0.32 and 0.28 for Prince Albert and Thompson, respectively.

completely due to differences in LAI and growing season (Table 2). Maintenance respiration is considerably less at Thompson compared to Prince Albert for both genera due to the colder air and soil temperatures. These results are similar to another recent model of boreal ecosystems (Bonan, 1991a, 1991b).

Total annual APAR for spruce was greater than for aspen. For aspen, PAR was absorbed only during the growing season, whereas for spruce, PAR is absorbed over the entire year (very



The y -intercept of the regression equations for spruce and aspen (Figure 6) in Prince Albert was greater than Thompson, as expected from Figure 2 due to increased length of the growing season. The year-to-year differences in average maximum air temperature, average minimum air temperature, or growing-degree days for each site were small and were not significantly correlated to the yearly differences in ϵ . The temperature effects on ϵ (from the temperature effects on maintenance respiration) were only discernable using the large temperature differences between Prince Albert, Saskatchewan and Thompson, Manitoba. Therefore, the use of a temperature gradient from the northern edge to the southern edge of the boreal forest may be an acceptable surrogate for studying how climatic change will affect boreal ecosystem processes.



CONCLUSIONS

These simulations using physiological parameters from the literature suggest a major role of maintenance respiration, especially from woody biomass, in the annual carbon budget of boreal forest ecosystems. There seems to be little variation in ϵ across the landscape caused by slope, aspect, and differences in the maximum available soil water content. However, there may be large differences in ϵ across the landscape due to the variations in LAI and stem biomass caused by different successional ages of the forest stands. Leaf area index (as well as APAR) can be

estimated with remotely sensed vegetation indices. With closed canopies, variations in stem biomass may be the most important variable across the landscape affecting ϵ to get NPP from remote sensing data. Perhaps synthetic aperture radar data can be used to remotely sense woody biomass (Ranson and Sun, 1992; Dobson *et al.*, 1992). Finally, simulated ϵ changed significantly from year to year due to interannual variability of climate, primarily precipitation; however, year-to-year variations in temperature may be important for other regions (Hunt and Running, 1992).

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